

Recording the free-living behaviour of small-bodied, shallow-diving animals with data loggers

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Summary

1. Time–depth data recorders (TDRs) have been widely used to explore the behaviour of relatively large, deep divers. However, little is known about the dive behaviour of small, shallow divers such as semi-aquatic mammals.

2. We used high-resolution TDRs to record the diving behaviour of American mink *Mustela vison* (weight of individuals 580–1275 g) in rivers in Oxfordshire (UK) between December 2005 and March 2006.

3. Dives to > 0.2 m were measured in all individuals ($n = 6$). Modal dive depth and duration were 0.3 m and 10 s, respectively, although dives up to 3 m and 60 s in duration were recorded. Dive duration increased with dive depth.

4. Temperature data recorded by TDRs covaried with diving behaviour: they were relatively cold (modal temperature 4–6 °C across individuals) when mink were diving and relatively warm (modal temperature 24–36 °C across individuals) when mink were not diving.

5. Individuals differed hugely in their use of rivers, reflecting foraging plasticity across both terrestrial and aquatic environments. For some individuals there was < 1 dive per day while for others there was > 100 dives per day.

6. We have shown it is now possible to record the diving behaviour of small free-living animals that only dive a few tens of centimetres, opening up the way for a new range of TDR studies on shallow diving species.

Key-words: invasive species, otter, seal, semi-aquatic, small mammal.

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Introduction

The last 20 years have seen dramatic advances in the field of animal biotelemetry, since the infancy of this field (Amlaner & Macdonald 1980), with the development of a wide range of data-logging and transmitting devices that can collect a variety of information (Kooyman 2004). Time–depth recorders (TDRs), data-loggers that record the depth of an animal as well as ambient temperature, are now standard research equipment used routinely in studies of marine vertebrate foraging (e.g.

Boyd 1997; Schreer, Kovacs & Hines 2001; Sims *et al.* 2005). For example, TDRs have been widely deployed on a range of marine mammals (e.g. seals, whales), birds (e.g. penguins, cormorants and alcid), reptiles (e.g. sea turtles and sea snakes) and fish. In some cases, detailed depth and temperature data, comparable with that measured by TDRs, can also be relayed via Argos satellite transmitters (e.g. McMahon *et al.* 2005; Myers, Lovell & Hays 2006) or relayed acoustically (Sims *et al.* 2006). In addition to TDRs, a range of other data-loggers can record parameters such as the acceleration of animals during swimming (van Dam *et al.* 2002), mouth opening associated with prey capture and breathing (Wilson *et al.* 2002), images of what the animals themselves are seeing (Davis *et al.* 1999) or the sounds that they produce,

for example while hunting (Watwood *et al.* 2006). The data collected by such devices have led to huge advances in understanding of the free-living behaviour of marine vertebrates (see Ropert-Coudert & Wilson 2005 for recent references).

There are inevitably constraints on the size of devices that can be attached to animals (e.g. for welfare reasons) and, consequently, increased miniaturization of equipment has led to an expanding range of species that can be studied. For example, first-generation TDRs were large analogue devices, with Gentry & Kooyman (1986) describing cylindrical TDRs of dimensions 0.2 m \times 0.053 m that weighed 1.5 kg in air. This large size constrained the first deployments to mammals as large as seals. Similarly some of the first satellite tags weighed many kilograms and so were deployed on very large species such as basking sharks (Priede 1984). The size of devices has been shown to have direct impacts on foraging success, with increased drag reducing fitness especially in small species that actively pursue their prey, such as penguins (Ropert-Coudert & Wilson 2005). However, there has been a progressive miniaturization of devices over the last two decades and currently available TDRs weigh only a few grams (e.g. Hays *et al.* 2004), although welfare issues remain in certain circumstances and TDRs remain too large to attach to many small diving animals (Wilson & McMahon 2006).

As well as the problem associated with size of TDRs, a second consideration concerns the resolution of depth data that can be collected, which has implications for the type of diving species that can be studied. It is essential that depth can be measured in sufficient detail to capture the key elements of an animal's diving performance. For deep divers, fairly coarse precision on TDRs may be sufficient. For example, many species of seal routinely dive to tens or hundreds of metres and measuring such dives with a precision of a few metres may be adequate to describe the nature of dives (e.g. depth and duration) (e.g. Beck *et al.* 2003). However, for shallower dives, increased precision is required. Recently, TDRs have started to capture dives of only a metre or so in marine animals such as seals and turtles (Hays *et al.* 2001; Greaves *et al.* 2005). However, this need for depth and duration to be measured with appropriate precision still creates problems for studies with semi-aquatic divers, such as otters, mink and platypus as such animals may typically only dive to a few tens of centimetres and dives will be short, possibly only a few seconds. The need for exceedingly precise measurements of depth means that, to date, there have been very few studies of the free-living diving behaviour of such small, shallow divers (Nolet, Wansink & Kruuk 1993), although the need for such studies has been recognized for a long time (Stephenson *et al.* 1988). However, technological developments now mean that studies on such divers may be possible. Here we describe the deployment of novel state-of-the-art TDRs on to American mink *Mustela vison* in the UK and describe how the resulting data can reveal aspects of their behavioural patterns

that could not be quantified using other approaches. Hence we identify a new tool for studying small, shallow diving animals.

Materials and methods

TIME-DEPTH RECORDERS AND TANK TRIALS

We used the CEFAS G5 TDR (CEFAS Technology Ltd, Lowestoft, UK). The G5 is a cylindrical TDR (31 mm length by 8 mm diameter) that weighs 2.7 g in air and 1 g in water, and is the most powerful TDR of its size available. The G5 has a (nonvolatile Flash) memory capacity of 8 megabits, and is capable of storing 693 000 data points at its maximum precision (12-bit A–D resolution). The TDRs recorded (temperature-compensated) depth with a nominal 0.03 m resolution with a full recording range of 100 m. The temperature sensors recorded temperature to a precision of 0.03 °C with an accuracy of 0.1 °C. Temperature sensors were calibrated in the range 4–34 °C, with a T66% (i.e. the time taken to reach 66% of the step change between two temperatures) of 28 s over this range.

To validate the ability of the TDRs to record shallow dives, we conducted a tank trial in which four of the TDRs used in the field were lowered into an outside tank (water temp *c.* 5.5 °C). To test the precision and response time of the TDRs, two types of 'dive' were simulated: TDRs were either lowered into the water from above the water surface and held at depth for between 10 and 60 s at depths of 0.3, 0.5, 0.7 and 0.85 m ($n = 188$), or TDRs were lowered to depths of either 0.2 or 0.85 m and raised immediately afterwards ($n = 216$).

DEPLOYMENTS ON FREE-LIVING MINK

As part of a long-term study into the ecology of American mink in the UK (Macdonald & Harrington 2003), TDRs were attached to individuals in Oxfordshire along the rivers Cherwell and Thames (approximate latitude, longitude: 51.62°N, 1.08°W). Using standard protocols mink were captured using single-entry, wire mesh cage traps (A. Fenn and Co., Redditch, Worcestershire, UK) set on floating rafts secured to the riverbank (Reynolds, Short & Leigh 2004), baited with rabbit or sardines. Traps were checked once a day, early in the morning. Captured mink were transferred to a wooden box (0.15 \times 0.15 \times 0.48 m) with a Perspex window for the induction of anaesthesia (described in Yamaguchi, Strachan & Macdonald 2002) and anaesthetized using isoflurane (IsoFlo: Schering-Plough Animal Health, Welwyn Garden City, Hertfordshire, UK) delivered via a vaporizer attached to a portable oxygen cylinder (Mathews, Honess & Wofensohn 2002). Following induction, animals were transferred to a face mask to maintain anaesthesia during the handling procedure. Animals were uniquely marked with subcutaneous PIT tags (MID Fingerprint, UK) and fitted with radio-collars (Wildlife Materials International,

Table 1. Details of the TDR deployments on mink. Note that for mink 299 there were no depth data due to physical damage to the pressure sensors (see Methods for details)

Animal ID	Sex	Weight (g)	River	Date equipped	Days of data	Mean (SD), min., max. Temperature (°C)	Dives recorded (<i>n</i>)
299	f	760	Cherwell	15 December 2005	4.0	31.5 (8.2), 3.1, 38.8	n/a
187a	f	580	Cherwell	23 January 2006	5.4	27.9 (8.8), 3.4, 38.0	497
325	f	830	Thames	16 February 2006	6.0	27.5 (4.6), 4.8, 38.3	2
337	f	620	Cherwell	18 February 2006	5.5	23.5 (6.0), 4.3, 36.1	789
187b	m	1275	Thames	18 February 2006	5.5	29.3 (4.2), 6.5, 38.1	6
274	f	600	Cherwell	5 March 2006	4.7	27.2 (7.3), 1.3, 38.3	99
313	f	790	Cherwell	6 March 2006	0.8	27.9 (7.3), 3.0, 37.8	68

IL, USA), to which the TDR had been attached. Animals were transferred to a plastic holding box for recovery before being released at the site of capture. Animal handling time during collar/TDR fitting ranged between 3 and 11 min (average 7) while recovery from anaesthesia took 11–24 min (average 14.7). Weight (in air) of the collar with the TDR was 18 g (< 4% of the body weight of the smallest individual in this study).

On the first deployment the TDR was simply tied (using 15-lb breaking strain monofilament line) and taped to the collar, leaving the pressure sensors exposed. On recovery this TDR was found to be badly damaged and there was no pressure data, presumably due to the physical damage to the sensor. Therefore on all subsequent deployments the TDR was encased in semi-flexible 9 mm plastic tubing. A hole was punched in the casing and positioned over the temperature sensor to allow direct water access and the end of the TDR containing the pressure transducer was recessed by approximately 5 mm within the plastic tube so that it also received a free exchange of water but was protected from direct impacts. The entire package was attached to the collar with monofilament line and secured with glue and tape. With this modified attachment method, all TDRs that were recovered showed minimal damage.

DIVE ANALYSIS

Dive profiles were extracted using MULTITRACE (Jensen Software Systems, Laboe, Germany), a bespoke software program for examining logger data-sets. We selected 0.2 m as the threshold for a dive event, i.e. only dives deeper than 0.2 m were extracted by MULTITRACE. This threshold was picked to show the ability of the TDR to resolve very shallow dives. All dives were viewed before the dive parameters (dive depth and duration) were accepted. We corrected the surface baseline for each dive. This baseline can drift away from zero (usually by a few centimetres) due, for example, to changes in atmospheric pressure, temperature or sensor drift. Setting the surface baseline to zero for each dive corrects for these effects and helped to ensure that the absolute depth values were accurate. All times are expressed in GMT. Approximate times of sunrise and sunset at the study site were 08.00 and 16.00 h during

December, 08.00 and 16.20 h during January, 07.20 and 17.20 h during February and 06.20 and 18.10 h during March.

ENVIRONMENTAL MEASUREMENTS

To give an indication of water and air temperature at field sites we deployed Tinytag Plus temperature loggers (Gemini Data Loggers (UK) Ltd, Chichester, UK). One temperature logger was deployed to record air temperature [at a height of 0.2 m on the river bank (attached to a tree trunk so partially sheltered)] and one deployed to measure water temperature (at an approximate depth of 0.1 m) on the River Cherwell. Both were set to record temperature at 1-min intervals and were left in place between 22 January and 1 February 2006.

Results

In tank trials the TDRs measured accurately the depth and duration of simulated shallow dives. The measured duration of the timed dives (*n* = 184) was always within 2 s of the timed duration (mean deviation = 0.36 s, range ± 1.6 s). The average deviation of the TDR measured depth from the actual depth on simulated dives was 1.3 cm (*n* = 404, range ± 5 cm).

We obtained a total of 31.9 days of data from seven mink between December 2005 and March 2006 (Table 1). For an eighth deployment, the TDR was not recovered. The details of each of the equipped animals are shown in Table 1. Air temperature measured in the study area during January fluctuated between night-time lows of −6 °C and daytime highs of +5 °C. Water temperature was more constant, varying between 2.5 and 5.5 °C. Collars were worn for a maximum of 13 days and within this period there was no neck abrasion, no visible evidence of collar irritation and all animals appeared in good body condition when recaptured.

In four of seven cases the logger memory was filled before the animals were recaptured. In one case the animal was recaptured while the logger was still recording data. In this instance we restricted data analysis up until the last point when it was known the animal was still at liberty (based on cold temperatures indicating

Table 2. Depth and duration of dives for the four mink for which > 10 dives were recorded, including the least squares fit regression equations relating dive duration (s) and depth (m)

Mink id	Dive depth (m) mean, median, max, SD	Dive duration mean, median, max, SD	Equation	r^2	Probability
187a	0.69, 0.58, 2.22, 0.41	14.9, 14.0, 47.6, 7.4	Duration = 12.8 depth + 6.07	0.50	$F_{1,495} = 493, P < 0.001$
337	0.44, 0.40, 1.79, 0.20	9.8, 9.0, 36.2, 4.6	Duration = 12.7 depth + 4.2	0.29	$F_{1,787} = 321, P < 0.001$
274	0.87, 0.59, 2.94, 0.70	14.0, 11.0, 40.0, 8.5	Duration = 9.9 depth + 5.4	0.66	$F_{1,97} = 189, P < 0.001$
313	0.59, 0.50, 1.54, 0.31	13.3, 11.4, 34.0, 6.4	Duration = 10.8 depth + 7.0	0.27	$F_{1,66} = 24.7, P < 0.001$

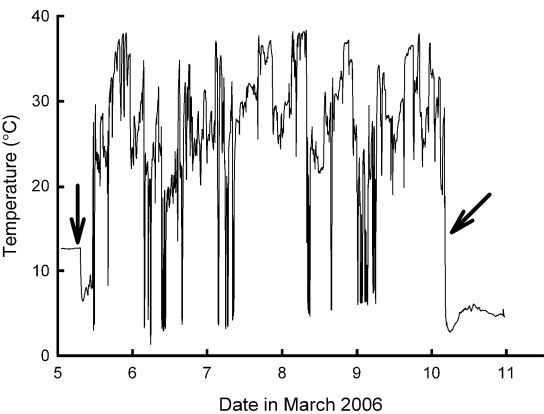


Fig. 1. Temperature data for mink 274 for which the collar was shed by the mink. Arrows indicate the time when the collar was deployed and then the inferred time when the collar was shed, based on the temperature stabilizing around a cold temperature. Also evident is the large fluctuation in temperature recorded while the TDR was attached.

the animal was in the water). In two other cases loggers were recovered from shed collars. In both cases the time that the collar was shed was clearly evident by the stabilization of cold temperature recorded by each logger (Fig. 1).

A general pattern of highly variable TDR temperature was evident in many of the deployments (Fig. 1). Maximum and minimum temperatures recorded were 38.8 °C and 1.3 °C for mink 299 and 274, respectively. However, values close to these extremes were recorded for all individuals (Table 1).

Often associated with the coldest temperatures were clear dive profiles. For example Fig. 2 shows a series of dive profiles recorded by mink 187a. However, even when diving, occasionally warmish temperatures were recorded. This observation seemed to reflect the thermal response of a warm TDR upon immersion, which will be a consequence not only of the sensor response time but also the mounting position of the TDR within the collar. The warm TDR temperatures recorded out of the water were presumably due to heat from the mink's body warming the tag.

Dives were recorded for all six of the mink for which we had depth data (Table 1), although for two individuals only a small number of dives were recorded. Diving rates varied hugely between these individuals with the average number of dives per day being 92.0, 0.3, 143.5, 1.1, 21.1 and 85.0, i.e. a near 500-fold variation across

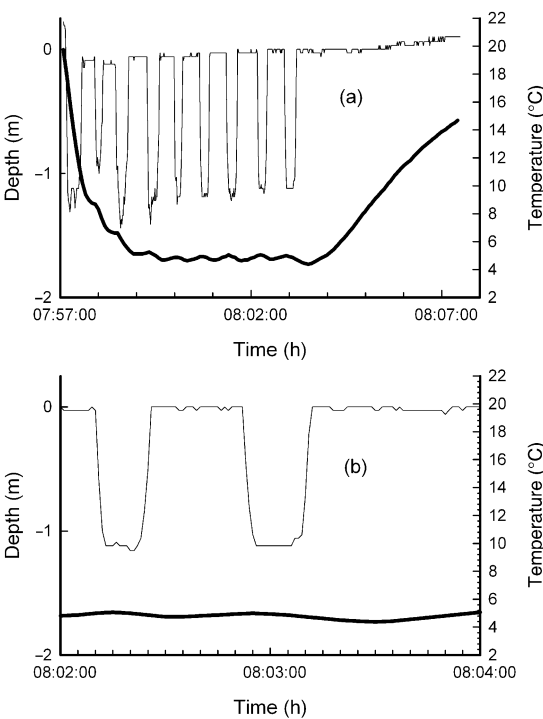


Fig. 2. To illustrate the low temperatures recorded while mink were diving, the dive profiles recorded by mink 187a on 27 January 2006. In panel (a) a series of nine dives (fine line) is shown along with the accompanying drop in temperature (heavy line) to about 5 °C. In panel (b) the last two dives in this series along with accompanying temperature are shown in detail. The baseline depth often shifted in association with the first dive in a bout, due to the large temperature change. To extract dive parameters (dive depth and duration) the baseline was set to zero at the end of such dives. This shifting baseline was much less evident once the TDR had stabilized at a cooler temperature.

the six individuals. Dives were typically 0.4–0.9 m in depth, but sometimes deeper than 1.5 m (up to a maximum depth of almost 3 m). Duration of dives were typically 9–15 s, although dives over 30 s were recorded for all four individuals that frequently dived (Fig. 3, Table 2). There were significant differences between these individuals in both their mean dive duration and mean dive depth (ANOVA, $P < 0.001$ in both cases), with mink 337 conducting relatively short and shallow dives and mink 274 conducting relatively deep dives. These significant differences were confirmed with nonparametric analysis of dive depth and duration across individuals (Mann–Whitney tests on median dive duration and

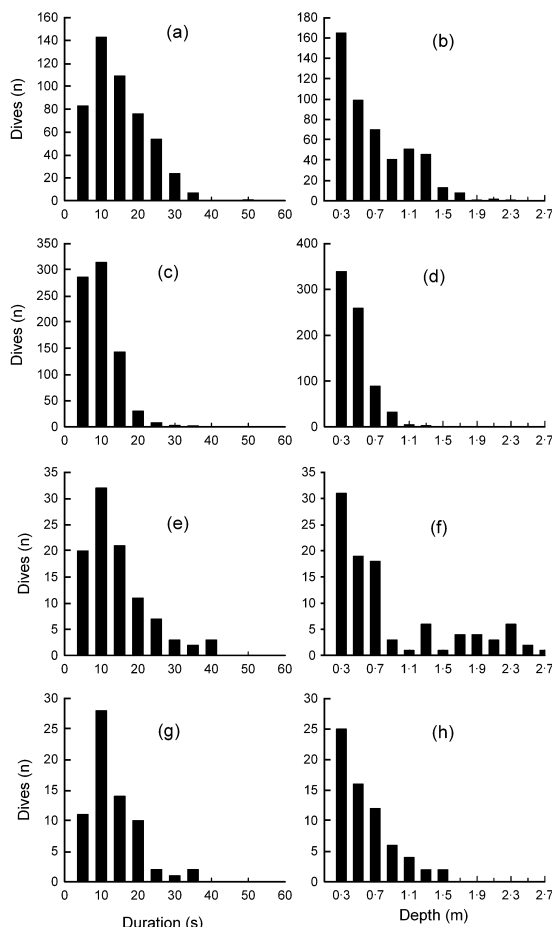


Fig. 3. For the four mink (187a, 337, 274, 313, respectively) for which we recorded dives, the frequency distributions of (a,c,e,g) dive durations and (b,d,f,h) dive depths.

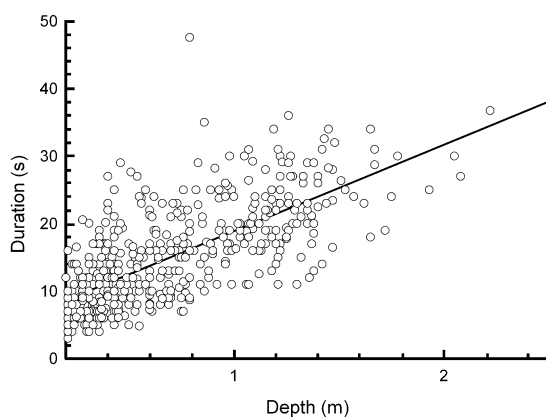


Fig. 4. The relationship between dive depth and duration for mink 187a. For the four individuals for which we recorded > 10 dives there was always a significant relationship between dive depth and duration (Table 2).

depth, $P < 0.001$). For the four individuals for which many dives were recorded, dive duration increased significantly with dive depth (Fig. 4 and Table 2).

There was a clear diurnal pattern to diving, with up to an average of 18 dives per hour being performed

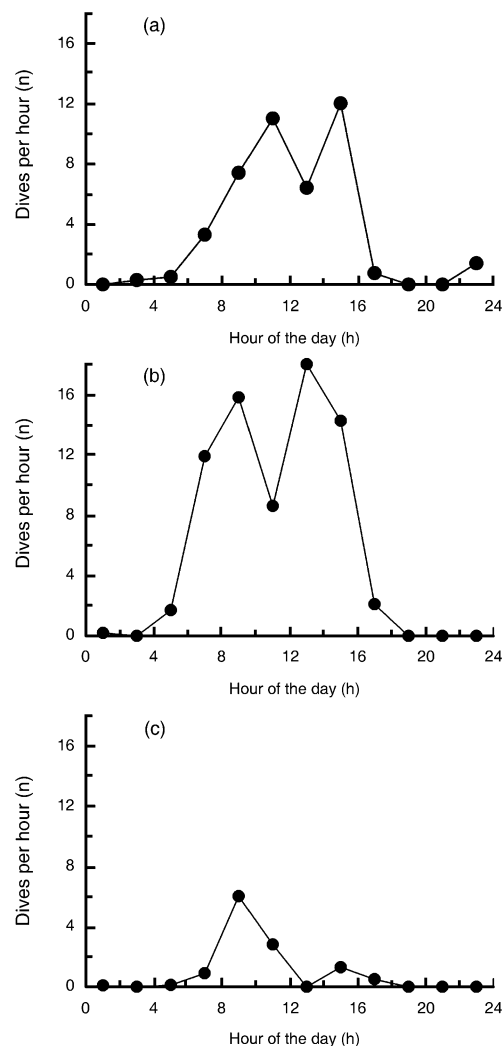


Fig. 5. Diel patterns in activity. The mean number of dives performed per hour for the three mink which performed the most dives. (a–c) Data for mink 187a, 337 and 274, respectively. No data are shown for mink 313 as although this mink performed many dives, this TDR stayed attached for less than 1 day.

during the day (Fig. 5). Also there appeared to be a consistent decline in diving activity during the middle of the day, separating morning and afternoon periods of activity. Diving generally occurred in discrete bouts. For example, Fig. 6 shows the timing of individual dives performed over 1 day. In between bouts of diving the TDR re-warmed.

Discussion

We have shown here that recording details of the behaviour of small-bodied, shallow diving semi-aquatic mammals on a second-by-second basis and over periods of several days is now possible using data-loggers. This methodological advance will open the way for a new era of studies on smaller animals that, to date, have not been amenable to data-logging studies. Despite the small sample size, a number of hitherto unknown aspects of

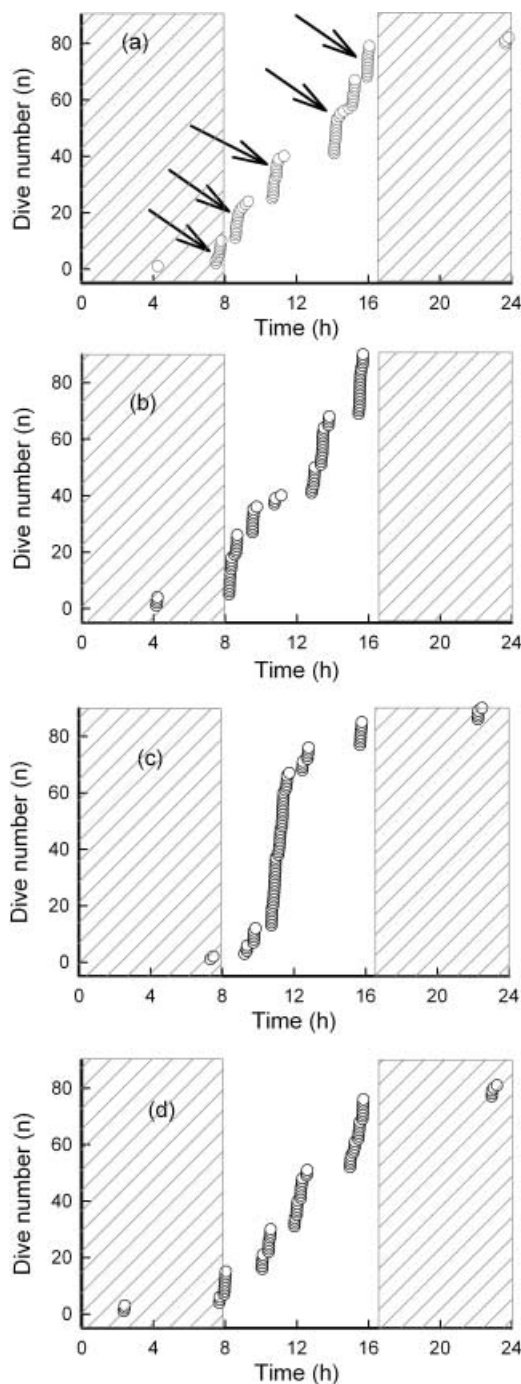


Fig. 6. To illustrate how diving typically occurred in distinct bouts, the timing of individual dives performed by mink 187a on particular days is illustrated. (a–d) Represent 24–27 January 2006, respectively. Number of dives performed on each day was 82, 106, 90 and 81, respectively. Dive number represents the cumulative number of dives performed on that day. Dives occurred in distinct bouts indicated by the continuous incrementing of the dive number without any gaps. On 24 January these bouts are indicated by the arrows. Hours of darkness are shown by grey shading.

Previous studies documenting the diving behaviour of free-living mustelids have used direct observations of highly visible individuals, such as otters *Lutra lutra* diving in the sea close to shore (Nolet, Wansink & Kruuk 1993). This approach clearly has limited utility in the situations it can be employed and in the extent of data that can be collected. For this reason, most studies on the diving behaviour of mustelids have focused on captive animals. For example, there have been a number of detailed studies of the diving behaviour of captive mink (Dunstone & O'Connor 1979; Williams 1983). In a laboratory setting, mean dive durations of 11.9 and 7.0 s were recorded by two individuals diving into a confined space (submerged pipes), while mean dive durations on unrestricted dives in a 0.3 m deep tank were 3.3 and 4.6 s for these same two individuals (Stephenson *et al.* 1988). However, no prey were available during these dives, leading Stephenson *et al.* (1988) to speculate that dives would be longer on dives in which prey were detected. Data recorded by the loggers during our study provide the first detailed information of mink diving behaviour under natural conditions and clearly illustrate that the depth and duration of dives performed by mink exceed those recorded during captive diving trials of mink. This observation highlights one potential limitation of captive studies attempting to describe free-living dive performance.

As well as opening the way for ecological studies of shallow diving species, data-loggers of the type we describe here also extend the potential for comparative studies that attempt to shed light on the physiology and evolution of diving in vertebrates. For example, dive depth and duration are parameters that are routinely used to examine how dive performance scales with body size (Schreer & Kovacs 1997). However such allometric studies have a paucity of detail for shallow diving species. We have shown that comparative studies can now move on to include species that dive only a few tens of centimetres.

We recorded very cold temperatures when animals were diving, suggesting that activity patterns might also be derived from temperature as well as dive data, as has also been shown for marine birds (Tremblay *et al.* 2003). However, the exact tag position (e.g. in relation to fur) will influence temperature readings and so needs to be considered in relation to the specific details of each deployment situation.

Unlike some mammals that hibernate or become dormant in the winter at high latitude, mink do not have specific adaptations for wintertime fasting (Mustonen *et al.* 2005). Hence mink are expected to remain active and continue hunting throughout the winter, but how they partition their time across different environments is not clearly understood (Gerell 1969; Birks & Linn 1982; Dunstone & Birks 1983). We showed that individual mink differed in the amount of time they spent in water. Several fish species, including perch *Perca fluviatilis*, roach *Rutilus rutilus*, eel *Anguilla anguilla* and minnow *Phoxinus phoxinus*, were identified in faecal deposits collected from a den site within the study area (unpublished data), clearly indicating

that some mink in this area were indeed actively foraging for fish at this time. Presumably there is a small-scale mosaic of terrestrial and aquatic environments available to mink, and individuals adapt and optimize their foraging to their immediate environment.

Recent evidence suggests that increasing competitive pressure exerted by otters in the UK cause dramatic changes in mink diet and habitat use (Bonesi & Macdonald 2004; Bonesi, Chanin & Macdonald 2004). It is plausible that competitive displacement of mink by otters foraging predominately at night, might facilitate the expression of a more diurnal activity pattern in mink although further, more detailed work is clearly required to investigate this intriguing possibility. In addition to the difference in behaviours between individuals, data-loggers revealed clear patterns in activity across the diel cycle. First, it was evident that diving occurred mainly, but not exclusively, during the day. Surprisingly mink are often considered to be predominantly nocturnal species (Dunstone 1993; Yamaguchi & Macdonald 2003; Yamaguchi, Rushton & Macdonald 2003). However, even within the day there was not a uniform pattern of aquatic use, but rather diving seemed to occur in distinct bouts. Typically mink that used the water a lot, spent between 1 and 2 h at cold temperatures and then re-warmed before the next bout of diving. Again the ability of data-loggers to reveal the temporal pattern of foraging highlights their value as a general tool for ecologists studying shallow diving animals.

Interestingly there has been speculation that the poor insulative properties of mink fur might severely limit the amount of time that can be spent in cold water (Williams 1986). However, our results present a different picture with extensive use of aquatic foraging by some individuals involving fairly long dives. The lack of thick insulation might therefore not be a consequence of a lack of selection pressure driving aquatic adaptations, but rather a compromise to allow both aquatic and terrestrial foraging. For example, the lack of long fur or thick subcutaneous fat deposits may provide several benefits for terrestrial foraging: the animal is relatively unencumbered for running and better able to hunt in confined spaces (e.g. small burrows) and also less likely to overheat when chasing terrestrial prey (Williams 1986).

In summary, we have shown the utility of data-loggers for examining the behaviour of small shallow diving animals such as semi-aquatic mammals. Refinements to this use of data-loggers will certainly occur as the approach is perfected, but even at this early stage the utility of this technique is clearly evident. The scene is now set for the wide use of such devices on a range of small, shallow diving species.

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